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UNIVERSITY OF NORTHERN COLORADO

Greeley, Colorado

The Graduate School

A DESCRIPTION OF LICHEN COMMUNITY STRUCTURE
AND THE IMPACTS OF SPRUCE BEETLE
DISTURBANCE IN NORTHWESTERN
COLORADO

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of
Master of Science

Anna Elizabeth Freundlich

Natural and Health Sciences
School of Biological Sciences

December 2019

This Thesis by: Anna Elizabeth Freundlich

Entitled: *A description of lichen community structure and the impacts of spruce beetle disturbance in Northwestern Colorado*

has been approved as meeting the requirement for the Degree of Master of Science in College of Natural and Health Sciences in the School of Biological Sciences

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ABSTRACT

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Spruce beetle disturbance has affected millions of acres of forest throughout North America and Europe, but thus far little research has investigated how this disturbance influences lichen communities. To address this problem, we studied lichen communities and habitat characteristics within 44 plots across a chronosequence of spruce beetle damage spanning 1996–2017 in northwestern Colorado. We found 82 species of lichens, few habitat differences among spruce beetle disturbance classes, and only the most recently affected plots (2012–2017) had significantly different lichen community structure relative to remaining areas. Two primary gradients explained the majority of variation of lichen community structure within our study area. The first gradient was related to forest location and substrate, with the positive end of the axis associated with the Routt NF, higher partially decayed wood, and more bare ground, while the negative end of axis one was associated with plots located in the Roosevelt NF which had higher lichen species richness, more heavily-decayed wood, and more lichen and plant understory cover. The second gradient described lichen community trends related to canopy closure on the positive end of the axis while higher wind speeds and heavily decayed logs were associated with the negative end of this gradient. We suggest that differences in habitat characteristics that we noted as related to spruce beetle

disturbance, were instead due to our sampling method and large plot size. Further we speculate that recovery of understory plants and subalpine fir may compensate for the loss of spruce, manifesting as minimal differences in forest structure and lichen community structure across beetle disturbance classes. Slow recovery times of lichens could have also inhibited our ability to detect a response to spruce beetle disturbance. Future researchers should further examine the response of lichens to spruce beetle response since this disturbance type will continue to affect native forests and associated organisms into the foreseeable future.

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While this project is the result of years of hard work, I would not have been able to achieve this goal without the support of many people. First, I would not have been able to finish this program without the support of my friends here in Greeley. I would literally have gone insane if I did not have the chance to unwind with you all and have some fun when we had free time in our busy schedules. I am so glad that I met you all and I feel that we have made lifelong friendships. I would also like to thank my family for their support. You have always been supportive and have inspired me to advance my education. Even if you do not always understand everything happening in my life, you have always been loving and kind to me. Finally, I would like to thank my advisor Dr. Emily Holt. From taking a chance on me when I had originally applied to a different project to then supporting me through the planning, field work, and finally the write-up of this project, I have learned so much from you. I am a better scientist, educator, and overall decent person by working with you for the past 2 ½ years. Thank you all so much.

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CHAPTER I

INTRODUCTION TO THE STUDY SYSTEMS: LICHEN BIOLOGY, SPRUCE BEETLE DISTURBANCE, AND LICHEN DISTURBANCE ECOLOGY

Summary

North American coniferous forests have undergone dramatic changes over the past few decades. More intense, prevalent outbreaks of native bark beetles, owing to milder winters and drier environments due to climate change, have dramatically altered many landscapes; once healthy forests have been replaced by stands of defoliated snags (Bentz et al. 2010). In Colorado alone, the spruce beetle has affected over 1.5 million acres of Engelmann spruce (*Picea engelmannii*) and Subalpine Fir (*Abies lasiocarpa*) forests over the past two decades (Colorado State Forest Service 2015). While scientists have studied impacts of bark beetles on plants and animals, little research has been conducted on lichen communities. This study will address how lichens have been affected by spruce beetles in northwestern Colorado and describe the general lichen community trends within this area.

Lichens – Biology and Importance

Lichens are composites of many organisms, including at least one fungal partner and one or more photosynthetic partners (photobiont), which can be either an alga or a cyanobacterium (Nash 2008). For most lichens, the main fungal partner is an Ascomycete and the rest of lichenized fungi contain Basidiomycete fungi as the structural fungi (Nash

2008). Recently, scientists have discovered that many ascomycete macrolichens also associate with basidiomycete yeast that are embedded within the cortex (Spribrille et al. 2016). While the main fungal partner provides the structure and support, the photobiont provides either glucose or sugar alcohols for itself and its fungal partner (Nash 2008). This association allows lichen to inhabit areas where it would otherwise be harsh for either organism to survive individually (Insarova and Blagoveshchenskaya 2016). Lichen are generally slow-growing symbioses that grow attached to trees, rocks, moss, soil, or can even remain vagrant on soil (Sancho et al. 2007).

Lichens are important components of forest ecosystems. They can facilitate nitrogen cycling (Campbell and Freden 2007; Marks et al. 2015), provide habitat for insects (Bokhorst et al. 2015), be used as nesting material (Hayward and Rosentreter 1994), and serve as forage for ungulates during winter when preferred food is scarce (Lafleur et al. 2016). Lichens can also be important in the field of human public health, as some species are used as bioindicators of air pollution, and historically lichens have been used in traditional medicine that could become more widely used in future applications (Ranković 2015). It is therefore of the utmost importance to study how a pervasive and devastating disturbance like beetle kill could be affecting lichen communities.

Description of Spruce Beetle Disturbance

Disturbance is important in maintaining diversity within our ecosystems. Whether from pathogens, weather events, or insects, disturbance events create varying habitats within our ecosystems that help to support many different species (Sousa 1984). In coniferous forests throughout North America, tree death by bark beetle infestations has historically been an important source of disturbance; spruce beetles typically attacked

previously weakened trees, such as those affected by windthrow or disease (Raffa et al. 2008). The periodic killing of these weakened trees would help maintain heterogeneity within these forests, allowing for different habitats and early-successional species to continue to survive (Sousa 1984). The main biotic driver of this disturbance in the subalpine spruce-fir forests, *Dendroctonus rufipennis*, is a bark beetle of the subfamily Scolytinae within the Curculionidae family. This species of bark beetle preferentially attacks Engelmann spruce (*Picea engelmannii*) trees and avoids subalpine fir (*Abies lasiocarpa*) (Six and Bracewell 2015). Spruce beetles roost in the boles of Engelmann spruce trees during reproduction and often kill the host tree; when they excavate their roosts, the developing beetles feed on the vascular tissue inducing extensive internal damage to their host trees and harmful fungi are introduced into the tree bole (Six and Bracewell 2015). In successfully invaded trees, individual trees die and become completely defoliated within 2 – 4 years (Bentz et al. 2010).

However, the frequency and intensity of bark beetle attacks has increased in recent decades (Raffa et al. 2008). In Colorado alone, the spruce beetle has affected over 1.5 million acres of Engelmann spruce forest over the past two decades (Colorado State Forest Service 2015). First, past management practices have made forests in the United States more susceptible to widespread beetle disturbance. Large areas of forest are comprised of older, even aged trees as a result of previous logging and fire exclusion; since bark beetles preferentially attack more mature trees, even-aged forests are highly vulnerable to widespread beetle disturbance (Berg et al. 2006).

This native disturbance has also become an epidemic for reasons related to beetle and spruce response to climate change. Under historic conditions, spruce trees could

successfully resist bark beetle attacks by forcing burrowing beetles from their tree boles through pitch tubes (Nash 2008). Instead of digging into the tree, the offending insect is caught in a mass of pitch and forced out of the trunk. Unfortunately, when trees are under stress, such as drought associated with climate change, trees have fewer resources to allocate towards these pitch tubes and are less likely to successfully fend off a bark beetle attack (Hart et al. 2014; Nash 2008). Trees are also less likely to survive a beetle attack when they are attacked by large numbers of beetles (Allen et al. 2010). With milder winters and higher occurrences of drought caused by climate change, beetle outbreaks have and will continue to be prevalent and severe (Hart et al. 2014; Raffa et al. 2008). Specifically, climate change has increased the frequency of drought and subsequently stressed spruce-fir forests, reduced the over-winter cold mortality of the bark beetles, and potentially increased the likelihood of spruce beetles completing their life cycle within one year instead of two (Allen et al. 2010; Bentz et al. 2010; Hart et al. 2014; Raffa et al. 2008). Raffa and others (2008) have predicted that these quicker development times and subsequently large beetle populations, coupled with weakened trees, will dramatically increase the extent and intensity of bark beetle outbreaks in the near future. It is of the utmost importance to learn about how ecosystems are affected by beetle kill as this disturbance type continues to impact our forests.

Bark Beetle Disturbance – Abiotic and Biotic Impacts

When trees die as a result of bark beetle outbreak, forest structure is altered. Large-scale tree mortality, as a result of bark beetle disturbance, increases the amount of light that reaches the forest floor (Gauslaa and Solhaug 1996), the amount of coarse woody debris (Klutsch et al. 2009), wind exposure (Boudreault et al. 2013b) and

evaporation (Biederman et al. 2014) within a stand, and can affect the timing and amount of snow cover in a forest (Perrot et al. 2014). Changes in the canopy and water uptake within a forest, as a result of bark beetle infestation, also have contradictory effects on the hydrology of impacted forests; more snow accumulates within areas affected by bark beetles due to the reduced canopy, while the increase in sun exposure can increase the amount of ablation occurring in beetle-impacted areas (Biederman et al. 2014; Boon 2009). Beetle-impacted forests also have reduced evapotranspiration immediately after attack (since the trees are not alive) which is shortly reversed within a few years as vegetation recolonizes the understory (Mikkelsen et al. 2013).

After the trees are killed and defoliated within a bark beetle affected area, the rest of the forest ecosystem can respond in dramatic ways. More grasses and herbs establish themselves, and previously light-limited tree seedlings begin to grow more quickly (Boucher and Meade 2006). Lignicolous fungal cover increases as they take advantage of the increased amounts of substrate available (Bässler et al. 2016). As the populations of beetles increase, woodpeckers and other beetle predators become more prevalent (Drever and Martin 2010). Forest use by some mammal species changes after forests are attacked by spruce beetle; elk and mule deer use are positively correlated with bark beetle activity in forests, while habitat use by rodents such as ground squirrels and chipmunks is negatively correlated with bark beetle activity (Ivan et al. 2018). Finally, the fungal and insect communities within the tree boles are quite different; the fungi introduced by the bark beetles and local insects take advantage of the newly available tree snags (Allen et al. 2010).

Lichen Response to Logging and Fire Disturbance

While limited research has addressed how macrolichen communities react to bark beetle outbreaks, there is information on how macrolichen communities respond to other disturbance types within coniferous forests. In general, disturbed lichen communities are significantly different than communities in unaffected areas (Bartels and Chen 2015; Boudreault et al. 2013a; Johansson 2008; Price and Hochachka 2001). For example, fruticose epiphytic lichens (shrubby or hair-like lichens that grow on trees) have lower abundance in post-logged and fire-disturbed sites than controls (Boudreault et al. 2013b). In transplant studies, fruticose epiphytic lichen thalli transplanted into disturbed areas had lower growth rates than thalli transplanted into mature forests (Boudreault et al. 2013a). Studies have also shown that a sudden increase in light exposure, associated with disturbance, can harm lichen and inhibit photosynthetic activity for species not adapted to high light conditions (Gauslaa and Solhaug 1996), and increased wind exposure can increase thallus breakage of lichens (Boudreault et al. 2013b). While fruticose epiphytic lichens are negatively affected by disturbance, this trend may not be true for all epiphytic lichens. In a transplant study of the foliose (leafy) lichen *Lobaria oregana*, thalli had higher growth rates when transplanted into logged plots than the unlogged plots (Muir et al. 2006). These disparities may be due to a number of factors (e.g., dispersal limitations, environmental tolerances) and their interactions.

Terricolous (ground-dwelling) and lignicolous (wood-inhabiting) lichens, unlike epiphytic lichens, have demonstrated an overall increase in cover after disturbance in northern forests (Bråkenhielm and Liu 1998; Girard et al. 2017). Particular species, such as *Cladonia*, tended to do well after logging disturbance; their cover increased and they

had higher growth rates in newly opened areas compared to control plots (Boudreault et al. 2013b). This positive trend does have some exceptions. Terricolous lichens such as *Peltigera* and *Flavocetraria* are more likely found in old forests with closed canopies than in more open sites (Zouaoui et al. 2014). While different terricolous and lignicolous lichens responded to disturbance differently, many studies showed an overall positive response to logging and fire disturbance because of the overwhelming growth by *Cladonia* species (Botting and Freden 2006; Zouaoui et al. 2014). It is also possible that lignicolous lichens increased in abundance as the availability of coarse woody debris increases, which influenced the overall response of ground-dwelling lichens (Bässler et al. 2016).

Research Questions

Within this thesis, we broadly describe patterns of lichen community structure within northwestern Colorado. We also examined the potential effects of spruce beetle disturbance on forest structure and lichen communities along a chronosequence of disturbance. Using previous research on the effects of bark beetle disturbance on forest structure and research on lichen responses to canopy-clearing disturbance, we had several questions we will examine within our study.

- Q1 Are there differences in forest structure between areas affected and unaffected by spruce beetle disturbance?
- Q2 Are there differences in forest structure among areas more or less recently affected by spruce beetle disturbance?

Second, as a result of differing forest conditions, lichen communities in beetle-affected areas would be different from lichen communities in unaffected areas.

Furthermore, plots recently affected by spruce beetle would be different from areas less

recently affected by spruce beetle. We had the following questions related to lichen community structure:

- Q3 Are there differences in lichen community structure between areas affected and unaffected by spruce beetle disturbance?
- Q4 Are there differences in lichen community composition among areas more or less recently affected by spruce beetle disturbance?

CHAPTER II

INVESTIGATION OF THE IMPACTS OF SPRUCE BEETLE DISTURBANCE ON MACROLICHEN COMMUNITIES IN NORTHWESTERN COLORADO

Introduction

North American coniferous forests have undergone dramatic changes over the past few decades. More intense, prevalent outbreaks of native bark beetles, owing to milder winters and drier environments due to climate change, have dramatically altered many landscapes; once healthy forests have been replaced by stands of defoliated snags (Bentz et al. 2010). In Colorado alone, the spruce beetle has affected over 1.5 million acres of Engelmann spruce forest over the past two decades (Colorado State Forest Service 2015). While scientists have studied impacts of bark beetles on plants and animals, little research has been conducted on lichen communities. Therefore, we investigated whether lichen communities in beetle-affected forests had different lichen community structures based on time since spruce beetle disturbance.

When forests are attacked by bark beetles, environmental conditions within these forests can change substantially. In spruce-fir forests, past fire-suppression tactics and natural regeneration after disturbance have resulted in large areas of even-aged forest (Berg et al. 2006). When tree monocultures are attacked by bark beetle under optimal conditions, large areas of forest can be killed (Bentz et al. 2010). This large-scale tree mortality increases the amount of light that reaches the forest floor (Gauslaa and Solhaug

1996), the amount of coarse woody debris increases (Klutsch et al. 2009), there is more wind exposure (Boudreault et al. 2013b) and evaporation (Biederman et al. 2014) within a stand, and the timing and amount of snow cover can also be affected (Perrot et al. 2014). Changes in the canopy can have contradictory effects on the hydrology of impacted forests; more snow accumulates within areas affected by bark beetles due to the reduced canopy, while the increase in sun exposure can increase the amount of ablation occurring in beetle-impacted areas (Biederman et al. 2014; Boon 2009). These environmental changes, documented in other forests, could occur in the beetle-impacted forests of northern Colorado, and potentially influence its associated lichen communities.

Lichens are important components of forest ecosystems. They can facilitate nitrogen cycling (Campbell and Freden 2007; Marks et al. 2015), provide habitat for insects (Bokhorst et al. 2015), are used as nesting material (Hayward and Rosentreter 1994), and serve as forage for ungulates during winter when preferred food is scarce (Lafleur et al. 2016). Lichens can also be important in the field of human public health, as some species are used as bioindicators of air pollution, and historically lichens have been used in traditional medicine that could become more widely used in future applications (Ranković 2015). It is therefore critical to study how a pervasive and devastating disturbance like beetle kill could be affecting lichen communities.

At this current time, little information exists on the community response of lichens to bark beetle disturbance. To our knowledge, there are very few studies that study lichen response, either directly or indirectly, to bark beetle disturbance (Bässler et al. 2016; Beudert et al. 2015). Other related studies either investigate the effect of insect infestation on abiotic elements of the environment that minimally includes lichens

(Navrátil et al. 2019), focus on a single species' response (McCune et al. 2008), or investigate the impact of other disturbances but also consider lichen response due to overlap in forest cutting and beetle-kill impacts (Waterhouse et al. 2011). Bässler and others (2016) found that lignicolous lichens had higher species richness and abundance in areas affected by spruce beetle than in areas unaffected by spruce beetle. There are no studies that examine epiphyte response, terricolous response, or a holistic community response to bark beetle disturbance.

However, there is ample information on how macrolichen communities react to fire and logging disturbance within coniferous forests. We researched these disturbances because, like bark beetle disturbance, they reduce the amount of canopy cover relative to pre-disturbance conditions. In general, fire- or logging-disturbed lichen communities are significantly different than communities in unaffected areas (Bartels and Chen 2015; Boudreault et al. 2013a; Boudreault et al. 2013b; Johansson 2008; Price and Hochachka 2001). For example, fruticose epiphytic lichens have lower abundance in post-logged and fire disturbed sites than in control plots (Boudreault et al. 2013a). In transplant studies, fruticose epiphytic lichen thalli transplanted into disturbed areas had lower growth rates than thalli transplanted into mature forests (Boudreault et al. 2013a). While fruticose epiphytic lichens are negatively affected by disturbance, this trend is not true for all epiphytic lichens. In a transplant study of the foliose lichen *Lobaria oregana*, thalli had higher growth rates when transplanted into logged plots than the unlogged plots (Muir et al. 2006). These disparities may be due to numerous factors (e.g., dispersal limitations, environmental tolerances) and their interactions.

Terricolous and lignicolous lichens, unlike epiphytic lichens, have demonstrated an overall increase in lichen cover after disturbance in northern forests (Bråkenhielm and Liu 1998; Girard et al. 2017). After logging disturbance, particular species, such as *Cladonia*, increase in cover and have higher growth rates in newly opened areas compared to control plots (Boudreault et al. 2013b). This positive trend does have some exceptions. Terricolous lichens such as *Peltigera* and *Flavocetraria* are more likely to be found in old forests with closed canopies than in more open sites (Zouaoui et al. 2014). While different terricolous and lignicolous lichens react to disturbance differently, many studies show an overall positive response to logging and fire disturbance because of the overwhelming amount of growth by *Cladonia* species (Botting and Freden 2006; Zouaoui et al. 2014).

We had several objectives with this study. First, we investigated whether spruce beetle disturbance affected lichen community structure and whether lichen communities varied along a chronosequence of time since beetle disturbance. Second, we sought to broadly describe patterns of lichen communities within northwestern Colorado and relate them to the environmental conditions within our study area.

Methods

Study Area

Our study area included parts of the Engelmann spruce-subalpine fir forest of northwestern Colorado (40°21'8" - 41°1'5"N, 105°9'5" - 107°19'36"W; Figure 1). Our study area contained two forest units, Roosevelt and Routt National Forests (NF), separated from each other by a 50km wide valley. The Routt NF unit is bisected by the continental divide, while the Roosevelt NF unit sits just north and east of the continental

divide. Both forest units contain spruce-fir forest affected by spruce beetle; in general, the Routt NF was affected from 1996 – 2006, while the Roosevelt NF was affected from 2007 and continues through the present.

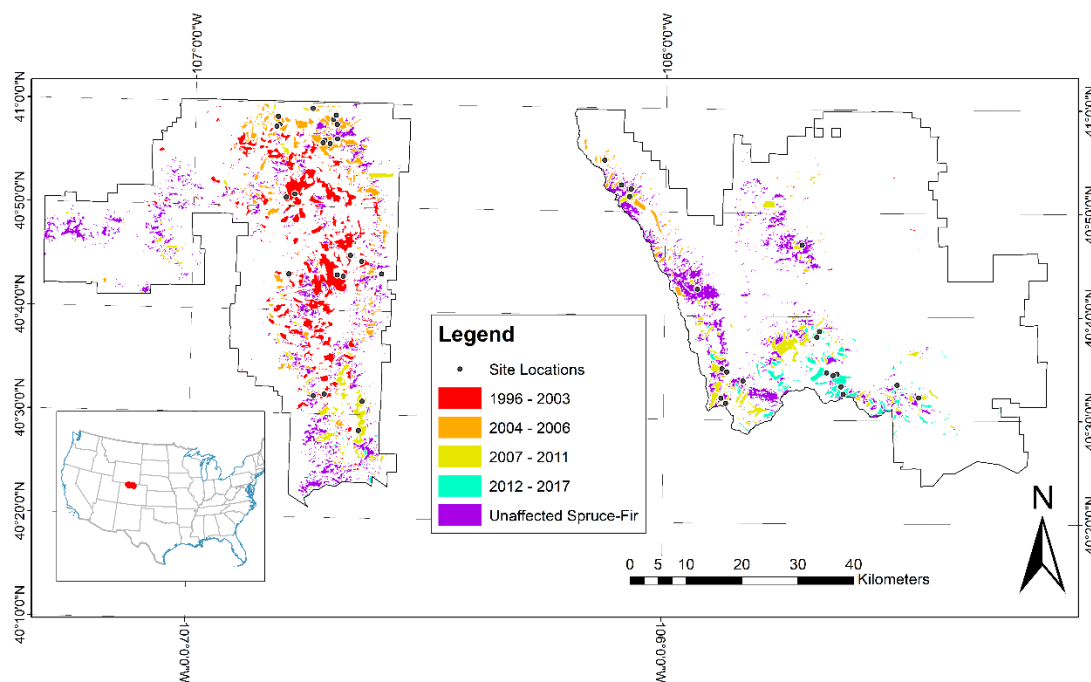


Figure 1: Study Design Map. Study area located in the Routt (left) and Roosevelt (right) National Forests in northern Colorado. Purple areas represent areas that were unaffected spruce-fir forest and colored areas were detected as affected by spruce beetles 1996 – 2017. Site locations are marked as black dots with a white outline.

Plots within both forest units were located within spruce-fir forests and had similar environmental characteristics; all plots were located at elevations (2,800 – 3,400m), experienced wind speeds (4-6 m/s), had average annual temperature ranges of 42-49 °C and forests were co-dominated by Engelmann spruce and subalpine fir (Fick and Hijmans 2017, Table 1). Understory communities were dominated by *Vaccinium scopulorum*, *Arnica cordifolia*, and numerous grass species (Pers. obs.). However, these two forests did differ in annual precipitation; weather typically moves west to east, bringing moisture from the Pacific Ocean (Kittel et al. 2015). The Routt NF, located

further west, receives more annual precipitation (81-170 cm) than the Roosevelt NF (48-120 cm), which is located further within the rain shadow of the southern Rocky Mountains (Fick and Hijmans 2017).

We selected this area over other spruce-fir forests in northern CO, because it was affected by spruce beetle (*Dendroctonus rufipennis*) to varying degrees in the 30 years prior to sampling; there was a robust lichen community present; and it was free of spruce budworm (*Choristoneura freemani*) at the time of sampling. Aerial Detection Survey data provided by the US Forest Service, based on aerial observer notes of needle discoloration (USDA Forest Service et al. 1996 - 2017), helped us determine the location and timing of spruce beetle attack within these spruce-fir forests (Ciesla 2006). Needle discoloration typically occurs the second or third year after initial infestation (Bentz et al. 2010), thus these aerial data were used to determine the approximate year of first infestation by spruce beetles.

Table 1: Mean characteristics of beetle disturbance classes. Associated variance (standard deviation in parentheses) is recorded with each characteristic. Significant differences between classes are marked with different lettered superscripts to signify differences. Unmarked variables or those with the same letter are not significantly different.

	1996-2003	2004-2006¹	2007-2011	2012-2017	Unaffected Spruce-Fir Forest
Sampling Design					
# of Plots Sampled	8	12	8	7	8
Forest Affiliation Routt:Roosevelt	8:0	9:3	2:6	0:7	3:5
Abiotic Characteristics²					
Elevation (ft)	9976.1 (670.1)	9805.3 (518.0)	9896.8 (585.6)	10180.3 (461.1)	10061.4 (262.9)
Water Cover⁴	1.1 (0.4)	1.2 (0.4)	1.4 (0.5)	1.1 (0.4)	1.4 (1.1)
Rock Cover⁴	2.7 (1.2)	2.2 (1.3)	1.8 (0.5)	3.6 (1.8)	2.5 (1.1)
Ground Cover⁴	3.3 (0.9)	3.2 (1.1)	3.1 (0.8)	2.1 (0.4)	2.9 (0.8)
Precipitation (cm)	139.4 (30.0) ^a	116.6 (22.6) ^{a,b}	94.7 (22.4) ^{b,c}	58.2 (7.1) ^d	103.4 (32.0) ^{a,b}
Mean Maximum Annual Temp (°C)	45.9 (2.5)	46.1 (1.7)	46.2 (2.7)	46.7 (2.1)	45.5 (1.4)
Mean Minimum Annual Temp (°C)	23.5 (1.2)	22.7 (1.6)	22.5 (2.0)	23.5 (2.1)	22.3 (1.5)
Mean Wind-speed 1984-2012 (m/s)	4.7 (0.5)	4.9 (0.5)	5.6 (0.5)	5.6 (0.8)	5.6 (0.5)
Slope (°)	5.7 (2.0)	5.1 (1.8)	5.9 (2.3)	7.4 (3.6)	4.5 (2.2)
Biotic Characteristics					
Understory Cover⁴	6 (0.7)	6.2 (1.0)	6.4 (0.5)	6.1 (1.2)	6.5 (0.5)
Lichen Cover – Trees⁴	2.8 (1.5)	3.3 (1.3)	3.4 (1.6)	2.7 (1.3)	3.4 (1.6)
Lichen Cover – Ground⁴	2.5 (0.5)	2.2 (0.4)	2.5 (0.8)	3.4 (1.6)	2.1 (0.6)
Fine Woody Debris⁴	2.9 (1.0)	2.9 (0.9)	2.8 (0.7)	3.3 (1.0)	2.6 (0.9)
Coarse Woody Debris⁴	3.75 (1.2)	3.8 (0.7)	3.6 (1.1)	4.3 (1.3)	3.4 (1.1)
Log Rank 1⁴	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
Log Rank 2⁴	1.25 (0.5)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	1.1 (0.4)
Log Rank 3⁴	4.9 (1.0)	4.7 (1.4)	3.5 (1.4)	2.9 (1.3)	3.8 (1.2)
Log Rank 4⁴	4.25 (0.9)	4.4 (0.7)	4.5 (0.9)	5.3 (0.8)	4.9 (0.4)
Log Rank 5⁴	3 (1.1)	3.4 (1.2)	4.1 (1.8)	4.3 (0.5)	3.8 (1.3)
Standing Wood Rank 1⁴	4.3 (1.2)	4.25 (1.1)	4.5 (0.5)	4.3 (1.3)	4.9 (0.6)

Table 1, Continued

	1996-2003	2004-2006¹	2007-2011	2012-2017	Unaffected Spruce-Fir Forest
Standing Wood Rank 2⁴	4.4 (0.9)	3.8 (1.1)	4.6 (0.5)	4.9 (0.9)	4.1 (0.6)
Standing Wood Rank 3⁴	4.1 (0.6)	4.7 (1.0)	3.4 (1.1)	3.7 (1.0)	3.9 (0.8)
Standing Wood Rank 4⁴	1.1 (0.4)	1.25 (0.5)	1.0 (0.0)	1.7 (0.5)	1.4 (0.5)
Standing Wood Rank 5⁴	1 (0.0)	1.1 (0.3)	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)
Engelmann Spruce⁴	3.6 (0.9)	3.3 (0.8)	3.4 (0.9)	3.6 (1.3)	3.9 (1.0)
Subalpine Fir⁴	6.1 (0.8)	6.2 (0.7)	6.4 (0.7)	5.9 (0.7)	5.9 (1.0)
Lodgepole Pine⁴	1.25 (0.9)	0.9 (1.1)	1.25 (1.0)	1.0 (0.8)	1.3 (0.9)
Basal Area (ft²/ac)	67.8 (15.1)	82.7 (12.1)	74.1 (12.2)	66.4 (20.2)	84.8 (10.6)
Diversity Measurements³					
Alpha Richness	11.0 (3.0) ^a	11.8 (3.1) ^a	14.3 (3.7) ^{ab}	16.7 (4.9) ^b	15.9 (4.5) ^{ab}
Beta Diversity	2	2.1	2.1	1.8	1.8
Gamma Diversity	36	38	48	55	45
¹ Averages do not include data from G2_S06, which was excluded as an outlier. One plot was removed from 2004-2006 beetle disturbance class so only 12 of 13 original plots are included in the statistics provided. ² Environmental variable summaries are not included here if standard deviation was less than 1 (n = 9), unless they were associated with strong correlation coefficients within the NMS ordination. ³ Diversity values were calculated using unmodified species data. ⁴ Values represented in the table represent coverage class values on the following scale: 1 = <1%, 2 = 1-5%, 3 = 6-10%, 4= 11-25%, 5= 36-50%, 6= 51-75%, 7= 76-90%, 8= ≥90%.					

Study Design

We developed a stratified random sampling design to determine plot locations.

Our sampling stratum was a spatially explicit data layer indicating beetle attack by chronology, and roughly balanced by area. First, we extracted 22 aerial survey data layers (USFS et al. 1996 - 2017) for each year available (i.e. 1996 – 2017) in ArcGIS 10.6.1 (ESRI 2018). From these data, we extracted areas that were affected by spruce beetle, i.e. areas of spruce-fir forest exhibiting needle discoloration. Areas were visually confirmed within a GIS that these beetle-affected areas were within spruce-fir forests. This

confirmation was done by comparing spruce beetle areas extracted from aerial survey data layers to a forest type data layer (US Geologic Survey Gap Analysis Program 2011). We then sought to create “beetle disturbance classes” to consolidate annual data into broader multi-year categories to increase manageability and minimize error. Since signs of infection occur over a period of several years, detection was sometimes inconsistent in sequential years; thus, grouping several years into classes helped minimize this error. Additionally, due to disparities in the total aerial extent of beetle kill each year and our goal to create roughly equal-area beetle disturbance classes, we clustered sequential years non-uniformly (Figure 2). Finally, four of our beetle disturbance classes composed sequential years of impact, balanced to contain roughly the same amount of forest area affected by spruce beetle: bark beetle attack detected in 1996 – 2003, 2004 – 2006, 2007 – 2011, and 2012 – 2017 (Figure 2). A final fifth class in our stratum was classified as unaffected forest, where no extensive damage was detected within spruce-fir forests from 1996 – 2017 (US Geologic Survey Gap Analysis Program 2011). Since spruce beetles are a native source of disturbance within these forests, all spruce likely experience some level of spruce beetle damage, but our “unaffected” areas contain forests which never reached epidemic levels that were detected remotely as were the forests in the four beetle disturbance classes.

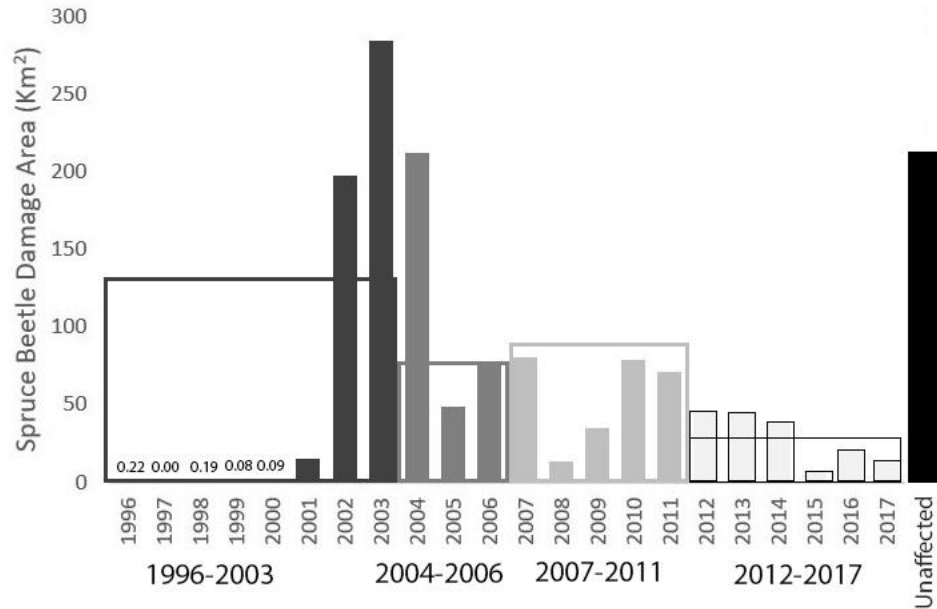


Figure 2: Spruce Beetle Damage Graph. Total area (km²) affected by spruce beetle, per year, within our study area are represented as filled bars or numbers, if less than 10 km² total of damage. Eligible unaffected area is represented as the final column in the figure. The hollow boxes represent the eligible sampling area for each beetle disturbance class; the width of each box depicts the years included within each class and the height indicates the total eligible area after applying a negative buffer of 35m to the polygons within each beetle disturbance class.

Within the aerial survey polygon layers (USFS et al. 1996 – 2017), areas were commonly marked as first impacted by beetles for more than one year. This detection pattern could be due to the subtle nature of the aerial signal or that needle discoloration within spruce-fir forest occurs for multiple years (Ciesla 2006). Although creating multi-year beetle disturbance classes helped minimize error associated with detecting first infestation in more than one year, it was still possible for an overlap in detection of first attack to occur in two classes. To maintain consistency, we only used forest areas that fell within one beetle disturbance class for our eligible sampling area. A negative buffer of 35m, roughly the width of our plots, was then applied to each beetle-disturbance class

polygon to further ensure that selected sites fit entirely within the areas of known beetle kill history.

We randomly generated 100 potential sampling locations (i.e. 20 sites per class) in a GIS within each beetle disturbance class and the unaffected forest category. Plots were deemed high priority from these generated points based on a combination of site accessibility (i.e., sites that were safe to access and no more than six miles from a trailhead) and proximity to additional sampling points. Fifty plots (i.e. 10 sites per class) were categorized as high priority while the remaining plots could be sampled if time allowed. In the field, we established the majority of plots within 50 m of the randomly generated point, but some had to be relocated due to inaccessibility to the original point, to avoid snow or water cover >25% within the plot, and to guarantee that plots would fall within forested habitat. We established 18 plots more than 50m away from their original randomly generated points; the furthest point was 1.3 km away from the original point.

Sampling Protocol

Lichen surveys were conducted within a 34.7m radius circular plot for a maximum time limit of two hours (McCune 2000). At each plot, we collected samples of all unknown macrolichen species encountered and then transported them to the University of Northern Colorado for further identification. We collected any foliose or fruticose specimens that were on the ground (i.e., decaying wood, rocks, and soil) and up to 2m in height above the ground on trees and boulders. A few species were field identified (5%), thus do not have associated herbarium vouchers. In addition, we visually estimated the abundance of each species using a cover class scale (i.e., 1 = 1-3 lichen thalli, 2 = 4-10 lichen thalli, 3 = coverage <1%, 4 = coverage 1 – 5%, coverage 5 = 6 –

25%, and 6 = coverage >26%; as per Holt et al. 2007). Species were identified in the lab using chemical tests and morphological keys (Goward 1999; McCune and Goward 1995). Thin layer chromatography was used to identify certain specimens within the genera of *Cladonia*, *Xanthoparmelia*, and *Solorina*.

At each plot, we recorded GPS coordinates and the elevation with a GPS unit at plot center. Slope and aspect was determined at plot center using a clinometer and a compass. All habitat measurements were determined visually within the plots, using cover categories: <1, 1-5, 6-10, 11-25, 26-50, 51-75, 76-90, or $\geq 90\%$, to closely mirror the logarithmic scale used for lichen abundance with added cover categories at the higher end of our scale. We measured the percent cover of total understory (i.e., vascular vegetation less than 0.5 m tall), overstory trees by species, snow, total lichen on trees, total lichen on the ground and rocks, rock, standing water, bare soil/duff, fine woody debris (i.e., distinguishable twigs and branches less than 8 cm in diameter), and coarse woody debris (i.e., wood larger than 8cm in diameter and stumps shorter than 1.5m tall). We categorize standing wood and logs into five decay rank (Table 2; adapted from Woodall and Monleon 2007), and then we estimated the abundance of wood within each decay rank using the same categories used for habitat cover. Logs were determined as fallen trees in contact with the ground for over 50% or more of their surfaces and were 8 cm or more in diameter. Further, snags (i.e., standing wood that is not a live tree) were defined as dead or dying trees that were still upright with less than 50% of their surfaces in contact with the ground.

Table 2: Snags and Log Decay Rank (Adapted from Woodall and Monleon 2007)

Trees, Snags, and Log Decay Rank	Descriptions
Rank 1	Healthy trees. Large and small branches are present on over 50% of the tree, foliated, bark is present, wood is hard.
Rank 2	Tree with healthy branches present on 50% or less of the tree, foliated, large branches and some small branches are still present, bark is present and wood is hard.
Rank 3	Tree with overall dead appearance; large and smaller branches are present but are not foliated, bark is starting to loosen, and some insect or woodpecker damage is present. Wood is generally hard, may be soft in some places.
Rank 4	Tree with large branches present, most of the smaller branches have been broken off the tree, branches are defoliated. Tops are typically broken off and at least 50% of the bark is loose or falling off the tree. The wood is soft and there are signs of obvious rot and insect damage, such as small exit holes in the trunk.
Rank 5	All the small branches have been broken off and the majority of larger branches have fallen, the branches are defoliated. Most of the bark is gone, exposing the wood underneath which is soft and losing its structural integrity. Snags in this class must be standing and taller than 1.5m in height. If they are shorter, they are considered stumps or coarse woody debris.

Basal area and canopy cover measurements were recorded at the plot center and at the north, south, east, and west edges of the plot perimeter. These five values were then averaged to yield overall plot measurements. Basal area, counting both live trees and snags, was recorded using wedge prisms, and canopy cover was determined using a spherical densitometer.

Analyses

The logarithmic nature of the lichen abundance classes eliminated the need to transform the data prior to conducting multivariate analyses. We then removed rare species (i.e., those occurring within only one plot; 37 species) to help clarify patterns within our data. One plot was removed from our dataset as it was more than two standard deviations from the grand mean of the average community distances.

Multivariate analyses were conducted within PC-ORD Version 7 (McCune and Mefford 2016). We used Non-Metric Multidimensional Scaling (NMS) to quantify relationships among plots without assuming gradients of community structure that

defined plot relationships. NMS was selected because our data did not follow linear, parametric assumptions, as is often encountered in community data, and zero values were frequent within our dataset, so it was important to select a statistical method robust enough to handle these absences (McCune and Grace 2002). NMS was conducted using the Autopilot mode on “Slow and Thorough” with the Sørensen distance measure, the most commonly used distance measure for community data (McCune and Grace 2002). We used a maximum of 500 iterations with 250 runs of real data to determine the best fit, defined as a solution with low stress and low instability.

We used Multi-response Permutation Procedure (MRPP; Mielke 1984) to determine whether groups were defined better by grouping variables than by random chance within our data (McCune and Grace 2002). We conducted MRPP comparisons on the lichen community data and our environmental variables. Euclidean distances were used to determine class and forest-level differences among environmental variables, while we used Sørensen distances to evaluate class and forest-level groupings of our lichen community data. Results were determined as statistically significant after applying a Bonferroni correction for multiple comparisons.

Finally, an Indicator Species Analysis (ISA; Dufrene and Legendre 1997) was conducted to determine the fidelity and frequency of lichen species occurring within preassigned groups. ISA helped us determine which species were indicative of each beetle disturbance classes. We also ran a randomization test, with 4999 runs, to discriminate significant indicator values from those simply arising by chance.

Results

We surveyed 44 total plots during summer 2018 (Table 1) and recorded a total of 82 species of lichens (Appendix 1). The most commonly encountered species were *Cladonia chlorophaea*, *Melanohalea exasperatula*, and *Usnea lapponica*. Prior to rare species deletions, the average species richness of each plot was 14.6 species and Whittaker's beta diversity of the sampling efforts was 4.6, suggesting moderate heterogeneity among plots.

Differences Among Beetle Disturbance Classes

We found weak but significant differences in lichen community structure across all beetle disturbance classes ($A = 0.04$, $p < 0.001$). Pairwise contrasts of lichen community structure among beetle disturbance classes yielded no significant differences ($p > 0.05$), except for a few notable exceptions. Specifically, the lichen communities of plots in the 2012-2017 beetle disturbance class were different from the plots in the 1996-2003 class ($A = 0.07$, $p < 0.001$), 2004-2006 class ($A = 0.07$, $p < 0.001$), and unaffected forest class ($A = 0.04$, $p = 0.02$). The 2007-2011 beetle disturbance class plots were the only ones not significantly different in lichen community structure from those impacted during 2012-2017 ($A = 0.02$, $p = 0.13$).

Indicator Species Analyses revealed that only five species were significant indicators ($p < 0.05$) for the 2012-2017 beetle disturbance class. These species were: *Melanohalea subolivacea*, *Physcia adscendens*, *P. stellaris*, *Vulpicidia pinastri*, and *Xanthoparmelia cumberlandia* (Appendix 1). These species had high fidelity within plots affected within the 2012-2017 beetle disturbance class and were quite rare within the

other disturbance classes. There were no significant indicator species for the remaining beetle disturbance or unaffected classes.

The majority of forest characteristics did not significantly differ between beetle disturbance classes ($p > 0.05$, Table 1). However, we did find a significant difference in annual precipitation among beetle disturbance classes ($A = 0.34$, $p < 0.001$). Because the 2012-2017 plots showed community differences to most other beetle disturbance classes, we also analyzed the environmental variables to compare the 2012-2017 plots to the remaining plots, as a single group, and we noted a similar pattern of homogeneity across plots. However, we did find that these 2012–2017 plots had significantly lower ground/duff cover ($A = 0.06$, $p = 0.02$), higher lichen ground cover ($A = 0.09$, $p = 0.002$), less cover of partially decayed logs (Log rank 3; $A = 0.05$, $p = 0.04$), more cover of intermediate-advanced decayed logs (Log rank 4; $A = 0.06$, $p = 0.03$), and lower annual precipitation ($A = 0.27$, $p < 0.001$) compared to all other plots combined.

Community Structure

The NMS ordination recommended by PC-ORD (McCune and Mefford 2016) was a 3D solution ($p = 0.004$; Figure 3). The best solution had a final stress of 17.81. The final instability was < 0.001 and 81 iterations were used in the final solution. The 3-axis solution explained 72.6% of the variance in lichen community structure.

The first axis explained 38.2% of the variance. The positive end of axis one was correlated with higher annual precipitation ($r = 0.743$), further west longitude ($r = 0.682$), higher cover of partially decayed logs (Log rank 3, $r = 0.576$), further north latitudes ($r = 0.469$), and higher cover of ground/duff ($r = 0.363$). The species most strongly positively correlated with axis one was *Cladonia fimbriata* ($r = 0.344$). Environmental variables

with the strongest negative associations to axis one were higher total lichen species richness ($r = -0.89$), higher cover of lichens on the ground ($r = -0.419$) and lichens on trees ($r = -0.396$), higher cover of heavily decayed logs (Log rank 5, $r = -0.477$), closed canopies ($r = -0.429$), and higher maximum ($r = -0.499$) and minimum temperatures ($r = -0.45$). The species with the strongest negative correlations were *Melanohalea subolivacea* ($r = -0.718$), *Vulpicidia pinastri* ($r = -0.649$), *Cladonia sulphurina* ($r = -0.66$), *Parmeliopsis ambigua* ($r = -0.528$), *Bryoria fuscescens* ($r = -0.504$), and *Usnea lapponica* ($r = -0.499$).

The second axis explained 18.8% of the variance within the lichen community matrix. The environmental variable with the strongest positive correlation, albeit fairly weak, was canopy closure ($r = 0.307$). The species with the strongest positive correlations were *Peltigera malacea* ($r = 0.416$) and *Peltigera leucophlebia* ($r = 0.342$). Environmental variables with the strongest negative correlations to this second axis were the higher cover of heavily decayed logs (Log rank 5, $r = -0.368$) and faster average wind speeds ($r = -0.314$). The species with the strongest negative correlations were *Cladonia macrophyllodes* ($r = -0.624$), *Physcia adscendens* ($r = -0.452$), *Stereocaulon alpina* ($r = -0.38$), and *Vulpicidia pinastri* ($r = -0.35$).

The third axis explained 15.6% of the variance. While most associations with this axis were weak, the environmental variables with the strongest positive correlations were higher cover of overstory subalpine fir ($r = 0.395$) and higher understory plant cover ($r = 0.357$). Species with the strongest positive correlations were *Cladonia cariosa* ($r = 0.507$) and *Parmeliopsis hyperoptera* ($r = 0.426$). The environmental variables with the strongest negative correlations to axis three were higher maximum ($r = -0.399$) and

minimum temperatures ($r = -0.309$), higher lichen cover on the ground ($r = -0.338$), higher lichen cover on rocks ($r = -0.304$), and higher cover of overstory Englemann spruce ($r = -0.255$). Species with the strongest negative correlations were *Peltigera malacea* ($r = -0.597$), *Cladonia cariosa* ($r = -0.51$), *Cladonia macrophyllodes* ($r = -0.436$), and *Cladonia ecmocyna ssp. intermedia* ($r = -0.346$).

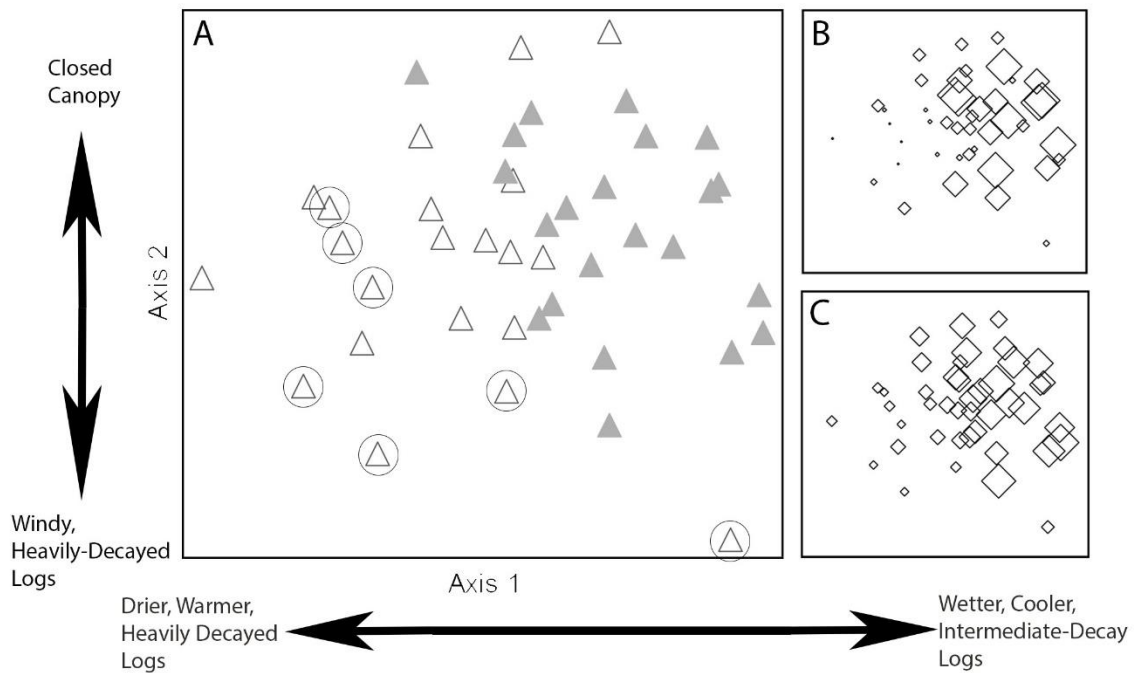


Figure 3: NMS ordination of the lichen community composition with three different overlays represented in the above panels. Each symbol represents one of our 44 plots. A 3D solution was recommended, but only two dimensions are shown here. In (A), Roosevelt plots are marked by open triangles, while Routt plots are marked by closed grey triangles. 2012 – 2017 beetle disturbance class plots are marked with open circles around triangles. In (B) the relative size of the diamonds represents the relative cover of intermediate decay of logs (Log rank 3), and in (C) the size of the symbol indicates the relative amount of precipitation.

Discussion

The following section will discuss the general patterns that describe lichen community structure throughout our study. Since we found a 3D solution, this means that there will be a separate discussion for each of the three axes that describe our lichen community patterns.

Axis 1: Geography/Substrate Axis

The primary ordination axis represents a geography/substrate gradient in macrolichen community structure. The driving forces behind this gradient are large-scale environmental conditions and geographical patterns. The two forests within our study area are roughly represented on opposing ends of axis one (Figure 3). Our sampling design constrained plots to spruce-fir forests, resulting in plots with similar elevations and tree canopy communities, but climatic variables differed between forests. Plots in the Routt National Forest (NF), located further north and west and situated near the continental divide, were wetter and cooler than plots in the Roosevelt National NF, which were located in the southern and eastern portions of the study area (Figure 1). Patterns in precipitation are dictated by how moisture is introduced within the region; the majority of moisture in Colorado comes from the Pacific Ocean to the western side of the state (Abbs and Pielke 1986). As these systems move eastward across the mountains, precipitation is released along the western slope and mountaintops with little moisture remaining for the eastern portions of the mountains and plains (Baron and Denning 1993). The geographic locations explain the climatic patterns between plots within the Routt NF and those in the Roosevelt NF, to which lichens were clearly responding along this axis. Similar trends of large-scale patterning of geography and climate has been found to affect lichen

community structure in a number of other studies (e.g., Esseen et al. 2016; Giordani and Incerti 2008; Marini et al. 2011).

Axis one also represents a substrate availability and suitability axis. In the species-rich Roosevelt plots, there was more heavily decayed wood (Log rank 5) and less open ground, while the less speciose Routt plots had more open ground and partially decayed wood (Log rank 3). Research has repeatedly shown that lichens can have strong preferences for particular substrates; specifically, that larger wood in advanced stages of decay harbor higher species richness and are more favorable for lichens than smaller, partially decayed wood (Dittrich et al. 2014; Humphrey et al. 2002; Kumar et al. 2017; Santianello et al. 2017). On the other hand, cover of open ground within sites could be indicative of soil habitat suitability. Assuming that areas suitable for lichens and/or vascular plants should be colonized, there should be less open ground in areas conducive to lichen and/or vascular plant establishment. If the underlying soil is not suitable, we would assume that these areas would not be colonized and remain open ground. Therefore, areas with more open ground and lower diversity, like what we observed in the Routt NF, may reflect lack of suitable substrate or terricolous habitat. These patterns of lichen diversification with more substrate availability within forest systems have also been supported by other studies (Crites and Dale 1998; Dittrich et al. 2014; Holt et al. 2015).

Axis 2: Canopy Fragmentation Gradient

The second axis corresponds to a canopy fragmentation gradient. The lichen response along this gradient reflects their sensitivity to increased solar radiation and the drying conditions of wind that could be a product of open canopies and resulting higher

wind speeds. *Peltigera leucophlebia* and *Peltigera malacea* are associated with the closed canopy end of axis two and often specialize in older, contiguous forests (Zouaoui et al. 2014), while other lichens (e.g. *Cladonia* spp.) favor more open areas (Bråkenhielm and Liu 1998; Boudreault et al. 2013b; Botting and Freden 2006; Girard et al. 2017; Zouaoui et al. 2014). Beyond altering direct incoming solar radiation, canopy fragmentation can also increase susceptibility to wind damage. On forest edges, alectoroid lichens experience more fracturing and are present in lower quantities than interior forest habitat (Esseen and Reinhorn 1998). Lichens underneath open canopies could also experience more intense drying effects as a result of increased wind exposure, which could affect lichen establishment (Anstett and Coiner 2010). Axis two therefore represents differing local growing conditions, due to open or closed canopies, to which lichens in these forests respond.

Axis 3: Spruce/Fir Gradient

The third ordination axis corresponds to an Engelmann Spruce-Subalpine Fir gradient, where the highest and lowest overstory cover of each species oppose one another at the ends of axis three. While all our sampled forests were dominated by fir (Table 1), the relative proportions of spruce:fir, as determined by the contribution of both species, varied along this axis. Numerous other studies have found that tree-specific characteristics like bark roughness and pH influence lichen community structure of epiphytes (Holt et al. 2015; Rosabal et al. 2013; Spier et al. 2010). Interestingly, the lichens responding most strongly to this gradient in our sample were all terricolous, thus differences in the environment under these trees was a key driver of lichen response rather differences on the trees' surfaces.

Research has shown that leaf litter, like foliar nutrient properties (Richardson 2004) and decay rates, can vary by species; specifically, Bigler and Veblen (2010) found that Engelmann spruce litter decays more quickly than subalpine fir (half-life of 4 years compared to 19 years) and a higher litter load. As these needles decay, concentrations of dissolved elements in the soil are altered (e.g, Cu, Zn, Mn, Cd, and Pb; Lomander and Johansson 2001) and could impact lichen fitness and colonization success (Paul et al. 2009). Further, soil research has shown that overstory tree species can also alter soil characteristics, such as carbon and nitrogen availability, that could be important for lichen establishment (Finzi et al. 1998; Augusto et al. 2002). Lichens are quite sensitive to microclimatic conditions (Haughian and Burton 2018; López et al. 2016; Nash 2008), and differing conditions around each tree species and under each differing litter load could differ enough to support different lichen communities. Plant and microbe community structure vary under different tree canopies (Behara and Misra 2006; Ister and Gokbulak 2009; Nilsson et al. 2008; Svenning and Skov 2002; Urbanová et al. 2015) and there is some support that terricolous lichens can be influenced by tree species (Kořuthová et al. 2013). Our observations along this spruce-fir gradient represent a similar pattern for lichen communities, largely comprising terricolous species, in northwestern Colorado.

Finally, while this spruce-fir gradient signals direct effects of the dominating overstory trees on terricolous lichens within these forests, this gradient likely also reflects competition between vascular plants and lichens. Other research suggests that in areas that have higher abundances of understory plants, ground-dwelling lichens are outcompeted (Cornelissen et al. 2001; Löbel et al. 2006). We found greater abundance

and frequency of ground-dwelling taxa, including *Peltigera malacea*, *Cladonia ecmocyna*, and *Cladonia macrophyllodes*, in plots with lower cover of understory plants. When cover of understory plants was high, the key lichen associates were wood-inhabiting species like *Parmeliopsis hyperoptera* and *Cladonia cariosa*, which may be able to avoid competition by occupying substrates that are not colonized by vascular plants (i.e. not soil). Less competition from understory plants at one end of this gradient, under canopies with a higher spruce:fir ratios, could also reflect less favorable conditions for vascular plant communities, which indirectly releases lichens from competition. Future research is needed to explore the factors that could contribute to the ill-suitability of canopies with more spruce cover for vascular plants, like soil chemistry, litter depth, and microclimate. These conditions, in turn, could clarify the relative contribution of direct effects of overstory tree identity on lichens versus the effects of competition between understory plants and lichen communities under different forest canopies.

Bark Beetle Impact - Countering Expectations

Prior literature of spruce beetle-kill effects on lichens (Bässler et al. 2016) and other canopy opening disturbance effects on lichens (Bartels and Chen 2015; Botting and Freden 2006; Boudreault et al. 2013a; Boudreault et al. 2013b; Lafleur et al. 2016; Zouaoui et al. 2014), led to our prediction that spruce beetle disturbance would impact lichen communities within northwestern Colorado. We expected that associated forest structural changes, noted elsewhere for beetle impacted forests, would precipitate these community shifts. We, however, did not observe these differences in forest structure in our study area, as are documented elsewhere. We propose two explanations for why our

sampled plots did not show these forest structure differences, which both would require further work beyond the scope of this study for confirmation.

First, our forest type could potentially mask beetle-induced structural changes. Spruce-fir forests in North America are co-dominated by Engelmann spruce (*Picea engelmannii*) and Subalpine fir (*Abies lasiocarpa*). When these forests are attacked by bark beetle, only mature spruce trees are killed (Bentz et al. 2010; Deroose and Long 2007; Veblen et al. 1991). However, spruce and fir trees are not evenly distributed throughout the landscape and often depend upon previous disturbance (Mietkiewicz et al. 2018). Since these two species share an ecological niche, individuals of both species will occupy habitat vacancies and utilize resources as they come available. Other spruce-fir forests affected by spruce beetle have transitioned from spruce-dominated to fir- or aspen-dominated forests (Deroose and Long 2007; Veblen et al. 1991). This shifting mosaic of overstory conifers in forests with more than one dominant species may act as a buffer to drastic forest structure changes often associated with beetle-kill in single-species dominated forests (e.g., Lodgepole pine; Cichewski and Williston 2004; Creeden et al. 2014; Klutsch et al. 2009; Perovich and Sibold 2016).

Second, the size of our sampling units could have obscured structural changes documented elsewhere associated with beetle epidemics, such as coarse woody debris or canopy cover. Other studies that report structural differences used much smaller sampling units (0.05-0.1 ha), and they also targeted canopy gaps produced as a result of beetle disturbance (Bässler et al. 2016; Winter et al. 2015; Winter et al. 2017). Our larger plots often contained both impacted spruce trees and healthy fir trees. Furthermore, we used a random stratified sample to increase our capacity to extrapolate patterns to the entire

study area and we relied on remotely sensed data rather than local site observations to locate plots. While our sampling methods were chosen because they align with protocols used with lichens in numerous past studies (e.g., Geiser and Neitlich 2007; Holt et al. 2009; Peterson and McCune 2001) and to increase the inference of our findings across the landscape, they may have been less than ideal to capture forest structure differences to the scale of this heterogeneous disturbance.

Overall, we did detect some differences in lichen community structure and environmental conditions among our disturbance classes. Lichen community structure of plots in the 2012-2017 beetle disturbance class were unique compared to most of the other disturbance classes; these plots received less annual precipitation, had higher lichen ground cover, lower cover of bare ground, and higher cover of intermediate and advanced decay logs (Log rank 3 and rank 4; Table 1). However, it is unclear if these differences in lichen community structure and associated environmental conditions are due to spruce beetle impact.

In forests affected by spruce beetle, understory forbs and tree saplings can respond quite quickly to canopy openings, which could then compensate for the loss of the overstory spruce trees (Berg et al. 2006; Pec et al. 2015). However, it is unlikely that measured differences in lichen community structure, only detected within six years of the infestation (i.e., 2012-2017 beetle disturbance class), are a result of rapid response and subsequent recovery to spruce beetle disturbance in six years. Lichens are slow-growing organisms and are difficult to detect until propagules have grown for several years (Bartels and Chen 2015; Girard et al. 2017), so it is unlikely that the indicator species for this disturbance class established themselves so recently after spruce beetle disturbance.

Next, the environmental conditions that separated this disturbance class apart from the remaining plots are unlikely to be influenced by bark beetle outbreak, but rather are characteristics that are affected by large-scale, long-term patterns. Specifically, changes to regional weather patterns occurs over larger spatial scales than the patchwork of beetle-kill studied here, and severe wood degradation in this region often occurs over a greater time scale than six years since bark beetle disturbance in the 2012-2017 beetle disturbance class plots. Instead, we suggest that the 2012 – 2017 plots were different because of larger geographic and environmental patterns within our study area described above as our strongest gradient in community structure along axis one.

Accordingly, all 2012-2017 beetle disturbance class plots were restricted to the Roosevelt NF (Table 1), which have more suitable environments and habitats available for macrolichens (Figure 3). Additionally, the majority of 2012-2017 class indicator species had strong negative correlations with axis one, which is more indicative of their affinity to that particular geography/substrate than their ability to colonize and establish within six years. This uneven distribution of plots between forests was also apparent in the 1996 – 2003 disturbance class, as these plots were only located within the less favorable Routt NF (Table 1). However, this unbalanced sampling was difficult to avoid. As the spruce beetle epidemic traveled through northern Colorado, the beetles traveled from the west to the east. This resulted in older plots being concentrated within the Routt NF and more recently affected plots being concentrated within the Roosevelt NF. Therefore, the differences we measured in lichen community structure more likely reflected larger geographic and environmental patterns.

Overall, we are not confident that we were able to capture structural changes in forest structure associated with spruce beetle attack and subsequent impacts on lichen community structure. We detected weak differences in lichen community structure and environmental conditions between plots sampled shortly after initial spruce beetle disturbance (2012-2017) but not among beetle disturbance classes older than six years post-infestation. We suspect that these differences are an artifact of our sampling design and the forest type, and instead reflect large-scale differences in geography and substrate. We cannot be sure if a beetle disturbance signal was not detected due to recovery of understory subalpine fir trees or as a result of our sampling design that did not specifically target canopy gaps resulting from bark beetle disturbance. Since we were unable to measure differences in forest structure related to bark beetle disturbance, any patterns we noted in lichen community structure cannot be unequivocally tied to spruce beetle impact. We therefore recommend that future researchers further investigate how bark beetles could be impacting lichen communities in this forest type.

Studying the impact of spruce beetle disturbance in lichens is important because this and other bark beetle disturbances will continue to become more prevalent as climate change continues to alter environmental conditions within our forests (Bentz et al. 2010; Raffa et al. 2008). As temperatures warm, spruce beetle populations develop more quickly into mature beetles, fewer individuals die during winter diapause, and trees are more often drought-stressed and cannot fend off offending beetles (Allen et al. 2010; Bentz et al. 2010; Hart et al. 2014; Nash 2008). While research has shown that bark beetle disturbance has had impacts on other forest animals (Allen et al. 2010; Drever and Martin 2010; Ivan et al. 2018,) and plants (Boucher and Meade 2006), this study

illustrates that disturbance may not always have immediate impacts on every component of our forest ecosystems, or at least at the scale we measured.

Limitations and Future Directions

While we identify some novel trends in the current work, our study had several limitations. First, we were not able to detect changes in forest structure with our sampling protocol, likely due to the several reasons described above (e.g. sampling method, forest type). However, other studies, conducted within the same forests in northern Colorado, detected a disturbance signal from bark beetles (Veblen et al. 1991; Mietkiewicz et al. 2018). Prior disturbance has also been shown to influence subsequent bark beetle disturbance impacts, and this could have confounded a clear signal in our study (Mietkiewicz et al. 2018; Veblen et al. 1994).

Next, we did not investigate whether our study area had been affected by additional disturbances, such as fire, logging, or wind-throw events. The high overall cover, across all plots, of overstory fir (mean = 74.0, SD = 15.6) led us to suspect that these forests had been previously disturbed by factors other than beetles; mature spruce-fir forests are dominated by spruce trees, while younger forests or those recovering from disturbance are first dominated by fir trees (Derose and Long 2007; Kayes and Tinker 2011; Temperli et al. 2015; Veblen et al. 1991), and full recovery from fir to spruce dominance can take several decades (Derderian et al. 2016; Veblen et al. 1991). However, the impact of multiple disturbances on lichen community structure was outside the scope of our study. Research has shown that previous disturbance can determine how an area will be impacted by bark beetle outbreaks (Berg et al. 2006; Temperli et al. 2015;

Veblen et al. 1994), so future work on this topic could benefit from consideration of multiple disturbance types.

Finally, while studies have shown that forest structure can change within a few years after bark beetle disturbance (Deroose and Long 2007; Winter et al. 2015; Winter et al. 2017), potentially we sampled too recently after spruce beetle disturbance to detect notable differences. We recommend that future studies revisit this area at a later date to accommodate the slower response times of lichen communities. Considering that the longest time since disturbance was 20 years and previous work has shown that lichen establishment is not detected until 7 – 15 years after disturbance (Bartels and Chen 2015; Girard et al. 2017), our study could have detected lichen die-back but not lichen establishment.

CHAPTER III

SUMMARY OF SPRUCE BEETLE IMPACT ON LICHEN COMMUNITY COMPOSITION AND FUTURE DIRECTIONS

Bark Beetle Impact – Countering Expectations

Prior literature of spruce beetle-kill effects on lichens (Bässler et al. 2016) and other canopy opening disturbance effects on lichens (Bartels and Chen 2015; Botting and Freden 2006; Boudreault et al. 2013a; Boudreault et al. 2013b; Lafleur et al. 2016; Zouaoui et al. 2014), led to our prediction that spruce beetle disturbance would impact lichen communities within northwestern Colorado. We expected that associated forest structural changes, noted elsewhere for beetle impacted forests, would precipitate these community shifts. We, however, did not observe these differences in forest structure in our study area, as are documented elsewhere. We propose two explanations for why our sampled plots did not show these forest structure differences, which both would require further work beyond the scope of this study for confirmation.

First, our forest type could potentially mask beetle-induced structural changes. Spruce-fir forests in North America are co-dominated by Engelmann spruce (*Picea engelmannii*) and Subalpine fir (*Abies lasiocarpa*). When these forests are attacked by bark beetle, only mature spruce trees are killed (Bentz et al. 2010; Deroose and Long 2007; Veblen et al. 1991). However, spruce and fir trees are not evenly distributed throughout the landscape and often depend upon previous disturbance (Mietkiewicz et al. 2018). Since these two species share an ecological niche, individuals of both species will

occupy habitat vacancies and utilize resources as they come available. Other spruce-fir forests affected by spruce beetle have transitioned from spruce-dominated to fir- or aspen-dominated forests (Deroose and Long 2007; Veblen et al. 1991). This shifting mosaic of overstory conifers in forests with more than one dominant species may act as a buffer to drastic forest structure changes often associated with beetle-kill in single-species dominated forests (e.g., Lodgepole pine; Cichewski and Williston 2004; Creeden et al. 2014; Klutsch et al. 2009; Perovich and Sibold 2016).

Second, the size of our sampling units could have obscured structural changes documented elsewhere associated with beetle epidemics, such as coarse woody debris or canopy cover. Other studies that report structural differences used much smaller sampling units (0.05-0.1 ha), and they also targeted canopy gaps produced as a result of beetle disturbance (Bässler et al. 2016; Winter et al. 2015; Winter et al. 2017). Our larger plots often contained both impacted spruce trees and healthy fir trees. Furthermore, we used a random stratified sample to increase our capacity to extrapolate patterns to the entire study area and we relied on remotely sensed data rather than local site observations to locate plots. While our sampling methods were chosen because they align with protocols used with lichens in numerous past studies (e.g., Geiser and Neitlich 2007; Holt et al. 2009; Peterson and McCune 2001) and to increase the inference of our findings across the landscape, they may have been less than ideal to capture forest structure differences to the scale of this heterogeneous disturbance.

Overall, we did detect some differences in lichen community structure and environmental conditions among our disturbance classes. Lichen community structure of plots in the 2012-2017 beetle disturbance class were unique compared to most of the

other disturbance classes; these plots received less annual precipitation, had higher lichen ground cover, lower cover of bare ground, and higher cover of intermediate and advanced decay logs (Log rank 3 and rank 4; Table 1). However, it is unclear if these differences in lichen community structure and associated environmental conditions are due to spruce beetle impact.

In forests affected by spruce beetle, understory forbs and tree saplings can respond quite quickly to canopy openings, which could then compensate for the loss of the overstory spruce trees (Berg et al. 2006; Pec et al. 2015). However, it is unlikely that measured differences in lichen community structure, only detected within six years of the infestation (i.e., 2012-2017 beetle disturbance class), are a result of rapid response and subsequent recovery to spruce beetle disturbance in six years. Lichens are slow-growing organisms and are difficult to detect until propagules have grown for several years (Bartels and Chen 2015; Girard et al. 2017), so it is unlikely that the indicator species for this disturbance class established themselves so recently after spruce beetle disturbance. Next, the environmental conditions that separated this disturbance class apart from the remaining plots are unlikely to be influenced by bark beetle outbreak, but rather are characteristics that are affected by large-scale, long-term patterns. Specifically, changes to regional weather patterns occurs over larger spatial scales than the patchwork of beetle-kill studied here, and severe wood degradation in this region often occurs over a greater time scale than six years since bark beetle disturbance in the 2012-2017 beetle disturbance class plots. Instead, we suggest that the 2012–2017 plots were different because of larger geographic and environmental patterns within our study area described above as our strongest gradient in community structure along axis one.

Accordingly, all 2012-2017 beetle disturbance class plots were restricted to the Roosevelt NF (Table 1), which have more suitable environments and habitats available for macrolichens (Figure 3). Additionally, the majority of 2012-2017 class indicator species had strong negative correlations with axis one, which is more indicative of their affinity to that particular geography/substrate than their ability to colonize and establish within six years. This uneven distribution of plots between forests was also apparent in the 1996–2003 disturbance class, as these plots were only located within the less favorable Routt NF (Table 1). However, this unbalanced sampling was difficult to avoid. As the spruce beetle epidemic traveled through northern Colorado, the beetles traveled from the west to the east. This resulted in older plots being concentrated within the Routt NF and more recently affected plots being concentrated within the Roosevelt NF. Therefore, the differences we measured in lichen community structure more likely reflected larger geographic and environmental patterns.

Overall, we are not confident that we were able to capture structural changes in forest structure associated with spruce beetle attack and subsequent impacts on lichen community structure. We detected weak differences in lichen community structure and environmental conditions between plots sampled shortly after initial spruce beetle disturbance (2012-2017) but not among beetle disturbance classes older than six years post-infestation. We suspect that these differences are an artifact of our sampling design and the forest type and reflect large-scale differences in geography and substrate rather than differences based on time since beetle disturbance. We cannot be sure if a beetle disturbance signal was not detected due to recovery of understory subalpine fir trees or as a result of our sampling design that did not specifically target canopy gaps resulting from

bark beetle disturbance. Since we were unable to detect differences in forest structure related to bark beetle disturbance, any patterns we noted in lichen community structure cannot be unequivocally tied to spruce beetle impact.

Studying the impact of spruce beetle disturbance in lichens is important because this and other bark beetle disturbances will continue to become more prevalent as climate change continues to alter environmental conditions within our forests (Bentz et al. 2010; Raffa et al. 2008). As temperatures warm, spruce beetle populations develop more quickly into mature beetles, fewer individuals die during winter diapause, and trees are more often drought-stressed and cannot protect themselves from offending beetles (Allen et al. 2010; Bentz et al. 2010; Hart et al. 2014; Nash 2008). While research has shown that bark beetle disturbance has had impacts on other forest animals (Allen et al. 2010; Drever and Martin 2010; Ivan et al. 2018,) and plants (Boucher and Meade 2006), this study illustrates that disturbance may not always have apparent impacts on every component of our forest ecosystems, or at least at the scale we measured.

Future Directions

The majority of ecological lichen studies thus far have been restricted to studying only specific components of lichen communities. For example, lichen disturbance studies in Canada often strictly study terricolous lichens that are important winter forage for caribou (Waterhouse et al. 2011; Boudreault et al. 2013b). Elsewhere, studies focus only on the response of single lichen species (Ignatenko and Tarasova 2018) or specific groups of lichens such as alectoroid epiphytes (McCune et al. 2008; Horstkotte et al. 2011), terricoles (Kořuthová et al. 2013; Zouaoui et al. 2014) or lignicoles (Bässler et al. 2016). However, studies such as these are insufficient when we want to understand the entire

lichen community due to their narrow focus. Forests are heterogeneous with many microhabitats available for lichen establishment. These habitats, in turn, can support diverse lichen communities that are sensitive to different environmental conditions. A holistic understanding of the lichen community requires an approach that studies all these potential microhabitats.

Even within a single forest canopy, distinct environments exist, each supporting different communities. Epiphytic lichens can vary along a vertical gradient; epiphytic communities closer to the ground are different from epiphytic communities in the mid or upper canopy (Kobylinski and Fredeen 2014; Fritz 2009; Campbell and Coxson 2001). The root of these disparities in epiphytes has been primarily attributed to differences in substrate quality and quantity (Crites and Dale 1998, Bässler et al. 2016; Dittrich et al. 2014; Santianello et al. 2017) or microclimate (Ódor et al. 2013; Rubio-Salcedo et al. 2015). Terricolous lichens, on the other hand, can be exposed to direct vascular plant and moss competition (Löbel et al. 2006; Cornelissen et al. 2001) and are sensitive to different soil types (Zouaoui et al. 2014). Terricolous lichens can also be buried under snowpack for large portions of the year, which can affect their photosynthetic activity and buffer them from temperature extremes, which is not true for epiphytic lichens growing above the snow pack (Bjerke et al. 2011). However, few studies have contrasted lichen responses from those on the ground to those in the trees (Botting et al. 2008; Boudreault et al. 2015).

Environmental conditions, such as temperature and humidity, can differ between the ground and canopy as distance above the ground increases (Campbell and Coxson 2001; Fritz 2009). Epiphytic lichens experience different environmental conditions than

ground-dwelling lichens, including increased wind exposure and solar radiation (Campbell and Coxson 2001; Fässler et al. 2014). Differences in conditions important for epiphytic and ground-dwelling communities are further illustrated by how these lichens oppositely respond to canopy openings (Boudreault et al. 2015). Studies on epiphytic lichens have found that disturbance-induced increases in solar radiation reduced photosynthetic activity of shade-adapted lichens (Gauslaa and Solhaug 1996), and that the distribution of epiphytic lichens was limited to areas with higher humidity, such as valleys or trees near bodies of water (Rambo 2010). Furthermore, higher wind speeds near forest edges increased fracturing and reduced the overall size of alectoroid lichens (Esseen and Reinhorn 1998; Esseen 2019). Studies of lichen response to logging and fire disturbance have found that, in general, epiphytic lichens responded poorly to these types of disturbances (i.e., slower growth rates and lower abundances) (Bartels and Chen 2015; Horstkotte et al. 2011).

In contrast, lignicolous and terricolous lichens respond quite differently to these same types of disturbances. Lignicolous lichens responded positively to disturbances that increase the woody debris available for colonization (Bässler et al. 2016). The majority of studies have shown that terricolous lichens, like *Cladonia* ssp., responded positively to logging and fire disturbance, through increased growth and cover as the canopy opens (Lafleur et al. 2016; Zouaoui et al. 2014; Boudreault et al. 2013b). However, many of these studies only focused on caribou food sources, so old-forest specialists, like *Peltigera* ssp., may respond differently to disturbances that reduce canopy cover. Generally terricoles community structure is driven by different factors (e.g. competition with plants and bryophytes, litter thickness, and microtopography; Boudreault et al. 2002)

than those important for epiphytes (e.g. solar radiation and humidity) or corticoles (e.g. woody debris). Overall, we expect that the community composition of downed wood- or ground-dwelling and epiphytic lichens differ due to the different environmental conditions they experience and their differential response to these conditions.

Studies into whether different components of lichen communities (e.g. epiphytes vs. lignicoles vs. terricoles) vary within a forest could also clarify the relative importance of microclimatic conditions and substrate. Numerous studies show that lichens often have specific preferences for substrates. For example, lignicolous species richness is often higher on larger, more severely decayed wood than smaller, less decayed wood (Caruso and Rudolphi 2009; Dittrich et al. 2014). Other studies have related lichen substrate preference to specific tree species (Asplund et al. 2014) and bark characteristics like roughness and pH (Jüriado et al 2012; Lamit et al. 2015). Overall, lichen substrate studies tend to focus on substrate-related traits and do not consider how environmental conditions could also influence lichen distributions. Studies that consider both substrate type and growth location within the forest could clarify whether the environmental conditions associated with the environment or the substrates themselves contribute more to lichen community composition. Future studies could begin to address these questions by concurrently examining lichen community structure of substrate-specific species (i.e. lignicolous, terricolous, and epiphytic lichens) and the community structure along a vertical gradient (e.g. lichens on the ground level vs. lichens in the trees). These types of studies are important to inform land management practices within lichen-rich forests. Understanding each components' contribution to the whole community response could allow land managers to more effectively conserve lichen communities. Lichens are

important components of our ecosystems, and better understanding of their diverse components can have positive impacts on the other organisms that rely on lichens for survival.

Summary

Overall, we detected some differences in lichen community composition and environmental conditions among our beetle disturbance classes within northwestern Colorado. However, we are not convinced that these differences are necessarily a result of spruce beetle disturbance. The variables that were detected as different are unlikely to be influenced by bark beetle disturbance. We also cannot conclusively determine that there was no influence of spruce beetle disturbance on lichen community composition because we could not detect a disturbance signal. Instead, we believe that larger geographic patterns and environmental conditions influence lichen community composition within northwestern Colorado.

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APPENDIX A

SPECIES INDICATOR VALUES, FREQUENCIES,
AND ABUNDANCE

Appendix A: Indicator values represent fidelity and abundance of each species. There are no indicator values for rare (1 plot) taxa, and significant indicator values are represented by *. Frequency represents the number of plots where a lichen species was detected. Frequency is the number of plots that contained each species. Average abundance represents the average abundance value of each species within plots where each lichen was detected.

Species Name	Indicator values	Frequency	Average Abundance
<i>Brodoa oroarctica</i>		1	1.00
<i>Bryoria chalybeiformis</i>		1	3.00
<i>Bryoria fremontii</i>	14.3	7	2.43
<i>Bryoria fusescens</i>	18.3	25	2.96
<i>Cetraria ericetorum</i>		1	1.00
<i>Cetraria islandica</i>		1	1.00
<i>Cladonia asahinae</i>		1	3.00
<i>Cladonia baciliformis</i>	5.6	4	2.25
<i>Cladonia cariosa</i>	24.9	29	2.45
<i>Cladonia carneola</i>	26.0	31	2.35
<i>Cladonia cenotea</i>		1	2.00
<i>Cladonia chlorophaea</i>	22.4	42	2.71
<i>Cladonia coniocraea</i>	21.7	34	2.38
<i>Cladonia decorticata</i>		5	1.60
<i>Cladonia deformis</i>	12.8	3	1.37
<i>Cladonia ecmocyna</i> ssp. <i>intermedia</i>	28.7	13	2.15
<i>Cladonia ecmocyna</i> ssp. <i>occidentalis</i>	15.2	6	3.50
<i>Cladonia fimbriata</i>	28.4	34	2.27
<i>Cladonia gracilis</i>		1	1.00
<i>Cladonia gracilis</i> subsp. <i>turbinata</i>		1	2.00
<i>Cladonia macilenta</i>	21.0	3	2.33
<i>Cladonia macrophyllodes</i>	14.4	21	2.90
<i>Cladonia merochlorophaea</i>	14.4	1	3.00
<i>Cladonia ochlorochlora</i>	7	5	1.40
<i>Cladonia pyxidata</i>	5.2	3	1.00
<i>Cladonia rangiferina</i>		1	0.10
<i>Cladonia sulphurina</i>	22.7	22	2.36
<i>Cladonia umbricola</i>		12	2.17
<i>Cladonia verruculosa</i>		1	1.00
<i>Dermatocarpon intestiniforme</i>		1	1.00
<i>Dermatocarpon moulinsii</i>		1	2.00
<i>Dermatocarpon reticulatum</i>		1	1.00
<i>Evernia divaricata</i>		1	1.00

Appendix A, Continued Species Name	Indicator values	Frequency	Average Abundance
<i>Hypogymnia austerodes</i>		1	1.00
<i>Hypogymnia farinacea</i>		1	3.00
<i>Hypogymnia imshaugii</i>	6.0	3	1.33
<i>Melanohalea exasperatula</i>	20.9	39	3.18
<i>Melanohalea subolivacea</i>	45.1* 2012 - 2017	9	3.33
<i>Nephroma parile</i>		1	1.00
<i>Parmeliopsis ambigua</i>	20.6	22	2.18
<i>Parmeliopsis hyperopta</i>	12.2	8	2.38
<i>Parmelia omphalodes</i>		1	1.00
<i>Parmelia sulcata</i>		1	1.00
<i>Physciella melanchra</i>	15.2	5	2.00
<i>Peltigera apthosa</i>	17.4	18	2.72
<i>Peltigera britannica</i>		1	3.00
<i>Peltigera canina</i>	14.8	5	2.20
<i>Peltigera collina</i>		1	2.00
<i>Peltigera didactyla</i>		1	2.00
<i>Peltigera horizontalis</i>		1	3.00
<i>Peltigera kristinsonii</i>	8.4	6	2.67
<i>Peltigera leucophlebia</i>	17.7	12	2.67
<i>Peltigera malacea</i>	18.4	26	2.55
<i>Peltigera neckeri</i>		1	2.00
<i>Peltigera polydactyla</i>	28.5	13	2.77
<i>Peltigera ponojensis</i>	6.7	8	2.88
<i>Peltigera praetextata</i>		1	2.00
<i>Peltigera rufescens</i>	7.3	7	2.43
<i>Phaeophyscia nigricans</i>		1	1.00
<i>Phaeophyscia orbicularis</i>	13.2	4	1.75
<i>Physcia adscendens</i>	39.5* 2012 - 2017	13	1.54
<i>Physcia biziana</i>		1	1.00
<i>Physcia caesia</i>		1	1.00
<i>Physcia stellaris</i>	42.3* 2012 - 2017	5	1.40
<i>Psoroma hyponorum</i>	26.6	19	1.74
<i>Rhizoplaca chrysoleuca</i>		1	2.00
<i>Rhizoplaca melanophthalma</i>	14.3	1	5.00
<i>Solorina crocea</i>		1	2.00
<i>Solorina octospora</i>		1	3.00
<i>Solorina saccata</i>	8.5	8	2.00
<i>Stereocaulon alpina</i>	9.1	2	2.00
<i>Stereocaulon myriocarpum</i>	7.5	2	1.00
<i>Umbilicaria hyperborea</i>	7.3	5	2.60
<i>Usnea cavernosa</i>		1	1.00

Appendix A, Continued Species Name	Indicator values	Frequency	Average Abundance
<i>Usnea lapponica</i>	24.4	40	3.05
<i>Vestergrenopsis elaeina</i>		1	1.00
<i>Vulpicidia pinastri</i>	34.9* 2012 - 2017	13	2.08
<i>Xanthoria elegans</i>		1	1.00
<i>Xanthoparmelia coloradoensis</i>	25.9	5	1.40
<i>Xanthoparmelia cumberlandia</i>	36.1* 2012 - 2017	7	2.86
<i>Xanthoparmelia lineola</i>	19.0	4	2.75